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A Field Study of a Vanishing Species, *Achatinella mustelina* (Gastropoda, Pulmonata), in the Waianae Mountains of Oahu[1]

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ABSTRACT: A population of *Achatinella mustelina* occupying four trees within a 5 × 5-m quadrat on a ridge in the Waianae Mountains of Oahu, Hawaii, was studied by mark–recapture techniques. Between September 1974 and December 1975, 222 snails were individually marked and measured. Recapture analyses indicate that the standing population consisted of about 220 snails, of which an average of 40 percent were large enough to be sexually reproductive. Growth of *A. mustelina* was found to be slow, averaging about 2 mm increase in length per year from a birth size of 4.50 mm to a size at terminal growth of 18.44 mm. Maturity is estimated to occur at an age of 6.9 yr. During the course of the study, snails belonging to the introduced predatory species *Euglandina rosea* were found progressively nearer the study site. In August 1979, shells of *E. rosea* were abundant in and about the study area and no living specimens of *A. mustelina* or any other arboreal snail species could be found. We conclude that *E. rosea* was responsible for the destruction of the population under study and that species with life histories similar to that of *A. mustelina* stand little chance of surviving the ravages of such introduced predators.

THE NATIVE LAND SNAILS of the Hawaiian Islands are rapidly becoming extinct, the victims of a host of human-related disturbances (van der Schalie 1969). Destruction of the snails' habitat and especially the native vegetation by logging, grazing, and competition with introduced exotic plants, the introduction of numerous predators, and extravagant removal by collectors (some of them scientists) have all taken their toll. The stylommatophoran subfamily Achatinellinae (family Achatinellidae), endemic to the Hawaiian Islands, was represented on the island of Oahu by 41 species of the genus *Achatinella* (Cooke and Kondo 1960, Pilsbry and Cooke 1912–1914). Now, fewer than half of these species survive and even these have become rare (Hart 1978, Kondo 1970).

Massive monographs have been written on shell variation in the achatinellids (Gulick 1905, Pilsbry and Cooke 1912–1914, Thwing 1907, Welch 1938, 1942), and their reproductive systems have been extensively studied, primarily for taxonomic reasons (Cooke and Kondo 1960, Pilsbry, Cooke, and Neal 1928). However, there is not a single study of these animals alive in their natural habitat, and only a single recent report discusses growth of animals maintained in the laboratory (Severns, in press). Even shell-size ranges in the large museum collections are missing from the conchological monographs. Thus, these snails, so admired by early adherents of Darwinism for their number of endemic species, are virtually unknown as biological entities.

The current study was undertaken to provide data on growth rate, age at reproductive maturity, size/age–frequency distribution, and such other demographic characteristics as might be learned from a field investigation of a population of *Achatinella mustelina* in the Waianae Mountains of west Oahu. We hoped that field-collected population data would contribute to an understanding of the reasons for the high

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extinction rates of *Achatinella* and suggest means for reversing them. At least the former goal was achieved.

The data presented were obtained via mark–recapture studies extending over a 3-yr period commencing in 1974. Few snails were removed from their habitat because of our conviction that even a small sampling program could lead to further population collapses.

METHODS

Study Site

The *Achatinella mustelina* population studied was located in small trees at an elevation of about 2400 ft near the trail to Puu Kanehoa on the eastern side of the Waianae Mountains, Oahu, Hawaii. This ridge contained one of only two relatively dense populations of *A. mustelina* seen during a fairly intense reconnaisance of their former wide range in the Waianae Mountains. The study site, a gently sloping, 5 × 5-m area, is near those designated as Kaluaa-Manuwaielelu ridge by Welch (1938). Snails were found here mainly on two *Osmanthus sandwicensis* and less frequently on a *Gouldia* sp. and an ohia lehua (*Metrosideros polymorpha*), the only trees in the quadrat. These trees were 5–7 m tall and somewhat sparse. Snails were located by visual searches of trunks, limbs, and leaves. Middle heights of the trees were searched by climbing; special care was taken to look for very small specimens. The highest parts of the trees could not be searched due to fragility of the limbs, and snails in these heights escaped collection. Ground cover in the study area consisted principally of leaf litter with some small scattered tufts of grass. Passion fruit vines were present on the ground and in some of the trees.

Species Studied

It is assumed here that all the snails observed can be assigned to the major Waianae Mountain species *Achatinella mustelina* Mighels, 1845. Many subspecies have been described from these mountains (Welch 1938), but for present purposes such designation is unimportant. A second species, *A. concavospira*, has been described from lower elevations on west Oahu, and some specimens from the current study site had characteristics of this species. However, given that the animals were sympatric, even to the tree limb, and no differences were seen in growth of animals belonging to these two potential species, all data are here considered together.

Marking and Measurement

The snails were assigned individual code numbers by cleaning a small area of the upper shell with cloth, applying a number with india ink, and, after the ink had dried, coating the number with a layer of clear, fast-drying lacquer (Decophane). Many of the numbers were clearly legible more than $2\frac{1}{2}$ yr after their application.

Achatinellids were removed from the trees, measured (length, width, and spire height above the aperture), assigned a code number, labeled, and, after all snails were measured, returned to the trees. Because retracted snails will not stick to limbs, animals were returned by putting them in small, open bags which were hung well up in the trees. Later recapture data indicate that the snails readily dispersed from these bags and none were ever found remaining in the bags on return visits to the study site.

Beginning in September 1974, all specimens of *Achatinella mustelina* found in the study area were marked and measured. On nearly monthly visits to the study site for the following 15 months, all snails recaptured were identified and remeasured and all previously unmarked snails found were measured and labeled. Subsequent visits were made to the study site in September 1976, January 1977, and August 1979, and all marked animals found were remeasured; no new snails were marked on these visits. Data were thus obtained on both individual growth rates and population size–frequency distributions at all seasons.

When animals were collected and marked,

other notations were made on color pattern, whether the animal better fit the apellation *Achatinella concavospira*, and whether the shell aperture possessed a thickened callus or "lip." Such a lip appears to indicate the end of growth in an achatinellid and probably also signifies the onset of sexual maturity (Pilsbry, Cooke, and Neal 1928).

Migration

The specific tree within the study area on which each snail was found was recorded at the time of collection. Because all snails were returned after each collection to a specific tree, it was possible to determine the frequency of migrations of snails from tree to tree. The data were examined to determine whether migration frequency was a function of time between recaptures or snail size.

Birth

Attempts to determine fecundity and other reproductive characteristics of *Achatinella mustelina* were limited by our reluctance to remove living animals from their native habitat. In September 1976, ten snails were collected near, but from outside, the study site and taken to the laboratory. They were kept in perforated plastic boxes under conditions similar to those utilized by Murray and Clarke (1966) for the culture of *Partula* spp. from Moorea. Freshly collected branches and leaves of *Osmanthus sandwicensis* and bark of ohia lehua were added to provide the epiphytic fungi upon which the snails feed. The specimens of *A. mustelina* survived well, and seven produced offspring within a month of collection.

Data Analyses

Altogether, 222 snails were measured and marked at the Kanehoa trail study site. Of these, 137 were recaptured at least once, the maximum number of recaptures being 11. Analysis of the population's size–frequency distribution was carried out by first collating the number of snails measured in each millimeter size class at each of 12 visits to the study site between 15 September 1974 and 20 December 1975 (Table 4). Then the percentage of the total number of snails represented by each size class was calculated and these were averaged across all 12 samples. The resultant histogram (Figure 3) thus represents the average percentage distribution of size classes over the major 15-month study period. Minimum and maximum sizes were also derived from these measurements and utilized to designate size at birth and maximum/reproductive size.

The size of the population of *Achatinella mustelina* was estimated in two ways from the mark–recapture data. First, the Lincoln Index (Poole 1974) was determined on the basis of the first mark–recapture set, wherein the estimated population size, $\hat{x}$, is the quantity found by dividing the product of the number of animals marked on the first visit, a, and the total number found on the second visit, n, by the number of marked animals recovered on the second visit, r:

$$\hat{x} = \frac{an}{r}$$

The variance for $\hat{x}$ is calculated as:

$$\mathrm{Var}(\hat{x}) = \frac{a^2 n(n - r)}{r^3}$$

The second estimate was arrived at by a linear regression of the percentages of marked snails caught at each visit against the total number of snails marked prior to each successive visit (Figure 4). Determining the value of 100 percent marked from the regression equation provided an estimate of total animals in the population.

Growth rate was analyzed in two ways. In the first method, data on the growth of ten snails for which six or more growth intervals were measured, representing the range of sizes of growing individuals of *Achatinella mustelina*, were subjected to regression analysis. The calculated slopes were averaged to arrive at a mean slope, expressed as millimeter increase per day, which is also a mean growth rate.

In the second method, all nonoverlapping

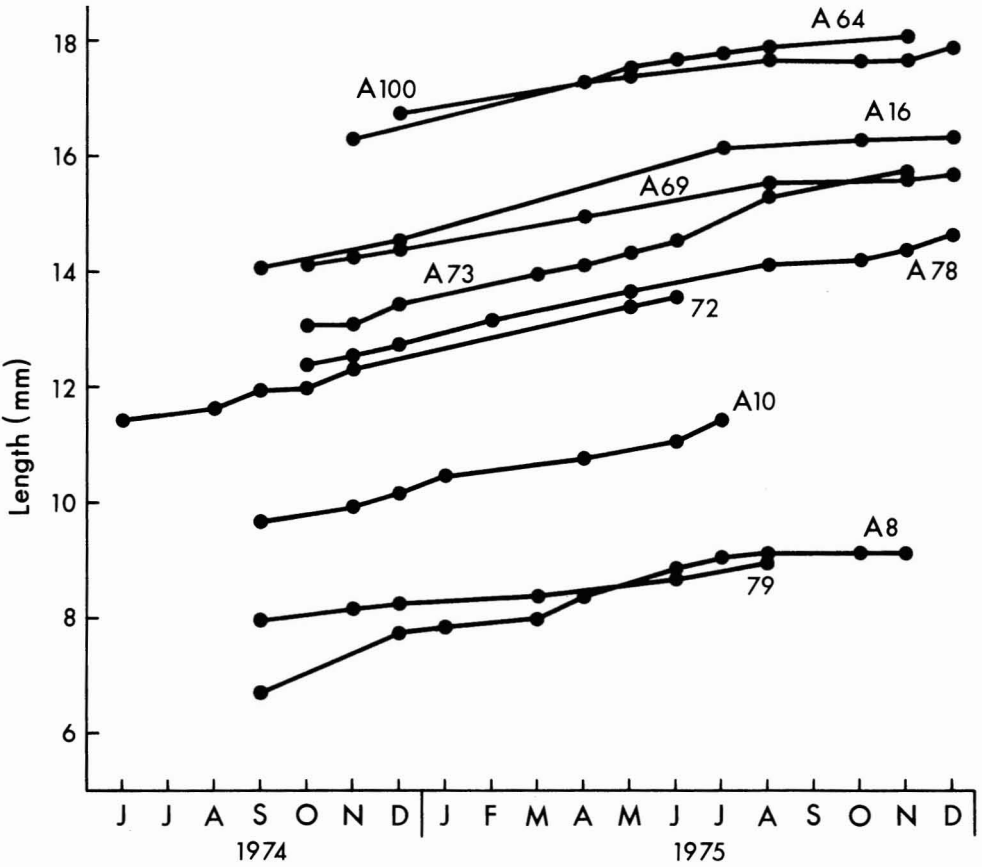

FIGURE 1. Growth curves for ten marked snails. Code numbers given for each snail are those used in the marking studies; regression slopes for these growth curves are presented in Table 1.

growth interval data for all snails were utilized to calculate growth rates. Thus, if one animal was measured twice, with an intervening time of 6 months, the growth rate over that 6-month period provided a single utilizable statistic. Other snails, measured up to eight times, with intervals of different durations, provided up to eight such rate measures. In calculating mean growth rates, the rate contributed by any one interval was weighted by multiplying it by the duration of the interval divided by the mean duration of all intervals so that short rapid bursts or brief lapses of growth were averaged out in final calculations. Because interval growth rates varied enormously, even for single individuals, it was considered better to handle the data in this manner than to calculate summary growth rates based on averages for individuals.

Growth was examined as an individual function and as a size function. From the calculated growth rates, ages were attached to size groups, and the age at reproductive maturity was extrapolated.

RESULTS

Growth

Growth curves for ten snails, chosen to represent a range of sizes among snails for which six or more intervals were measured and which did not have or develop a shell lip during the study, are presented in Figure 1.

TABLE 1

REGRESSION ANALYSIS OF GROWTH IN TEN *Achatinella mustelina*

SNAIL NUMBER	MIDLENGTH (mm)	SLOPE (mm × 10^{-3}/day)
A8	7.93	6.7
79	8.33	2.5
A10	10.54	5.4
72	12.49	6.1
A78	13.48	5.2
A73	15.365	8.6
A16	15.22	5.0
A69	14.89	3.7
A64	17.22	5.3
A100	17.34	2.9
Mean slope:	5.14 mm × 10^{-3}/day (SD = 1.81)	
Annual growth rate:	1.88 mm	

It is noteworthy that animals of all sizes appear to be growing at about the same rate. To determine whether this was indeed the case, a linear regression slope was calculated for each of the snails in Figure 1 (Table 1). As can be seen, there was no apparent correlation between slope and size. The mean value of the slopes gives a daily growth rate of 5.14 × 10^{-3} mm, or 1.88 mm/yr (SD = 0.66). From the data, it was concluded that the rate of growth in *Achatinella mustelina* is relatively constant throughout the growing portion of the life of the snail. Because this is unusual—most gastropods showing rapid early growth and a decreased rate of growth as size increases (Wilbur and Owen 1964)—further analyses of growth rate were carried out.

The second analysis of the pattern of growth consisted of entering all growth interval pairs for all animals in a simple linear regression model of growth rate versus mean size during the growth interval; 209 pairs were entered. The slope obtained did not differ significantly from zero.

Finally, all growth interval data were divided into three groups based on the mean length of the snail during the interval measured: below 10 mm; 10–15 mm; and greater than 15 mm. This segregation provided 24 snails (53 intervals) in the smallest size class, 27 snails (73 intervals) in the intermediate size class, and 32 snails (83 intervals) in the largest size class. Rates for each interval were weighted by the duration of the interval, and mean growth rates with standard deviations were calculated for each class. The results are presented in Table 2. Student *t*-tests show no significant differences among the mean growth rates of the three size classes. These statistical analyses provide an average growth rate of about 2.04 mm/yr for *Achatinella mustelina* of all sizes, a figure close to the one predicted for growth rate by regression analysis (1.88 mm/yr). Henceforth, an average growth rate of 2 mm/yr is assumed.

The smallest specimen of *Achatinella mus-*

TABLE 2

GROWTH RATE VERSUS SIZE IN *Achatinella mustelina*

ANIMAL LENGTH (mm)	NUMBER OF GROWTH INTERVALS	NUMBER OF SNAILS	AVERAGE GROWTH RATE (mm × 10^{-3}/day)	STANDARD DEVIATION
< 10.00	53	23	5.65	6.17
10.00–15.00	73	27	5.33	5.60
> 15.00	83	31	5.77	5.95
Mean growth rate (all sizes):			5.595 mm × 10^{-3}/day	
Annual growth rate:			2.042 mm/yr	

NOTE: Mean growth rates were determined by multiplying all individually measured growth rates (all possible intervals used for all animals) by a weighting factor consisting of the duration of the individual interval divided by the mean duration of all intervals measured. The mean growth rates, with their standard deviations, are calculated from the weighted interval rates.

TABLE 3

BIRTH SIZES OF SNAILS IN THE LABORATORY

SNAIL NUMBER	BIRTH DATE	BIRTH SIZE (mm)	PARENT (mm)
L1	9 September	4.54	18.83
L2	9 September	5.35	19.96
L3	11 September	4.30	18.27
L8	11 September	4.08	19.84
L4	18 September	3.27	18.92
L7	23 September	4.21	18.57
L10	5 October	3.28	18.44
Mean size at birth:		4.15 mm	

NOTE: Data on offspring of ten snails (L1–L10), collected on 4 September 1976.

telina found in the field measured 4.52 mm in length. Animals brought into the laboratory produced young measuring between 3.27 and 5.35 mm in length (see Table 3). Because laboratory conditions may induce premature birth (the smallest snails invariably died soon after birth), it is assumed that the smaller observed birth sizes in the laboratory do not reflect the normal situation. We thus take 4.50 mm as a better estimate of the average birth size of *A. mustelina* in the field (this figure is close to the mean size of laboratory-born juveniles, 4.15 mm; see Table 3).

It should be noted that the growth data cited refer to shell length, probably a poor measure of increase in animal mass. As an estimate of mass change with age, the length-to-width ratio (L/W) of 20 snails for each of three length classes (<10 mm, 10–15 mm, >15 mm) was calculated. The mean L/W was determined for each class and these means were compared by using t-tests. The results show highly significant differences: L/W for snails under 10 mm in length is 1.345; for snails 10–15 mm in length, 1.405; and for snails greater than 15 mm in length, 1.574. Since width of the shells does not accrue as rapidly as length, then neither does shell volume nor, presumably, mass. A negative exponential curve would probably better describe growth in weight of *Achatinella mustelina*.

Attainment of maximum size in achatinellas is marked by the formation of a thickened lip on the outer shell aperture (Pilsbry, Cooke, and Neal 1928). Animals with a thickened lip found in the present study varied in length from 16.69 to 20.40 mm (Figure 2). Snails that formed lips on their shells during the course of the study grew little or not at all after the formation of the lip, even though growth had been measured in these same individuals up to the time of lip formation. It was noted that a lip was developing in 27 animals during the study; mean length of these snails was 18.43 mm (SD = 0.755).

Age

An age at maturity can be determined by applying the average growth rate determined above; that is, the average size of snails with a shell lip, 18.43 mm ($n = 52$; SD = 0.78), minus the size at birth, 4.50 mm, gives a life growth of 13.93 mm. At a growth rate of 2.0 mm/yr, maximum size would be achieved in 6.9 yr. This age is also assumed to be that of animals at first reproduction.

Figure 3 presents the mean size–frequency distribution data for specimens of *Achatinella mustelina* in the study area. Age groups are also indicated. Age determinations are extrapolated as described above. A relatively even age distribution of snails up to a peak of abundance in the maximum size classes, apparent in Table 4, suggests continual reproduction (i.e., there are no apparent annual age groups) and a grouping of several years' progeny in the largest size category. There are suggestions of seasonality in the monthly distribution of occurrences of smallest animals, but the data are too meagre to make this clear (Table 4).

An examination of the recapture data shows that five marked animals with shell lips were present in the study area for at least 2 yr, and three lipped snails were present at collections spanning 28 months. Added to an estimated age at lip formation of 6.9 yr, we see a potential life-span exceeding $9\frac{1}{4}$ yr.

FIGURE 2. Shells of *Achatinella mustelina* chosen to illustrate the relative changes in shape that occur during growth from birth (the shell on the left) to maturity (the shell on the right). The length/width ratios of the five shells are, left to right, 1.16, 1.21, 1.25, 1.48, and 1.53. The largest shell bears a thickened lip, indicating terminal growth. Note that the shell in the middle is dextrally coiled, a character without taxonomic significance in this species. (The scale is graduated in millimeters.)

Population Size

The size of the population of *Achatinella mustelina* in the study area was not great. The number of snails seen there, located on each visit when exhaustive collecting was attempted, varied from 33 to 58 with a mean of 44 (Table 4). Of these, an average of 69 percent (range 27.6–90.5 percent) were recaptures and the remainder were animals measured for the first time. The lowest number of recaptures was on the second visit to the study site. On the single visits to the study site in 1976 and 1977, no new snails were marked. The number of recaptures, 33 and 24, respectively, suggests that the population was at about the same density as it had been throughout the more intensive part of the study. However, on the visit to the study site in August 1979, no living snails (marked or unmarked) were found in, or anywhere near, the study site, and the population was judged to be extinct. Seventy-four empty shells were collected beneath the trees; 15 of these bore evidence of our numbering, and 14 shells showed breakage of the sort attributed to rat predation.

The first estimate of the size of the population of *Achatinella mustelina* in the study area was based on the Lincoln Index, using first mark–recapture data (Table 4):

$$\hat{x} = \frac{58 \times 58}{16} = 210.25$$

$$\text{Variance of } \hat{x} = \frac{58^2(58)(58 - 16)}{16^3} = 2000.66$$

The standard deviation is found by taking the square root of the variance. The estimate for the population size is thus 210 $\pm$ 45 snails.

A second population estimate based on linear regression of the percentage of marked snails recaptured versus the total number of snails marked is shown in Figure 4. Extrapolating the percent marked to 100 gives an estimate of 234 animals in the population, or

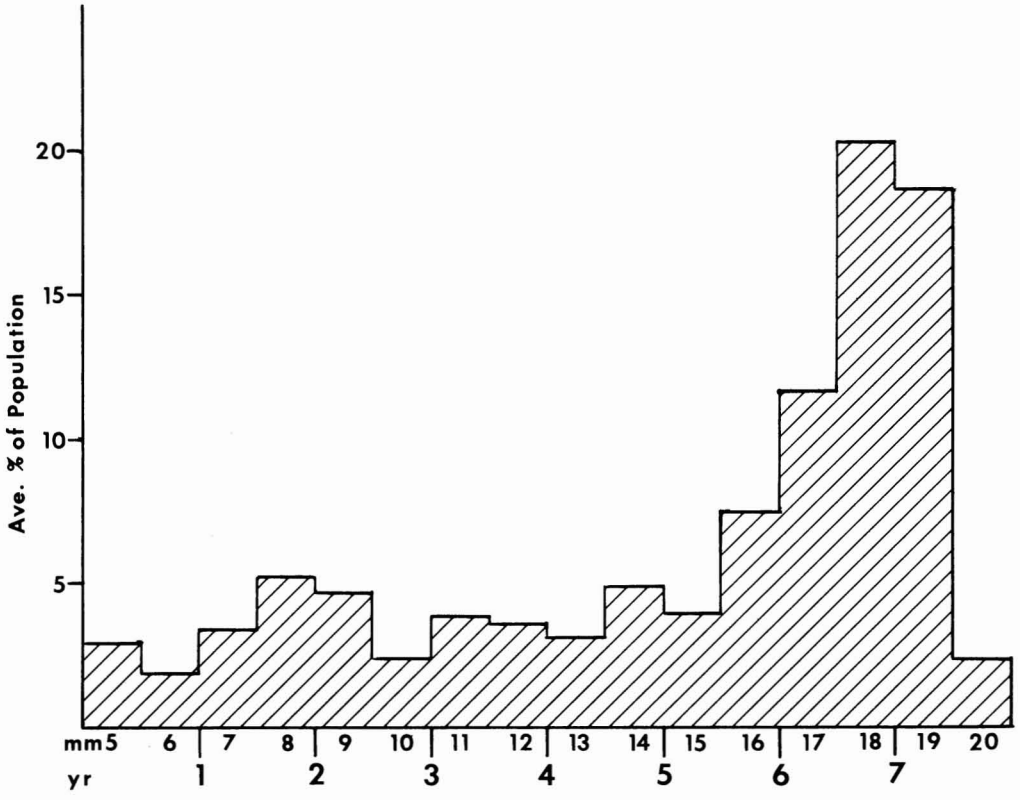

FIGURE 3. Size–frequency distribution in the study population of *Achatinella mustelina*. Sizes are expressed as millimeter class marks; ages are estimated from growth rate data. Each size class is shown as the average percentage of the total population it represented between September 1974 and December 1975. The monthly data are presented in Table 4.

215 if the last, somewhat anomalously low, recapture percentage (66.7 percent) is dropped. These estimates agree well with that obtained by the Lincoln Index. Estimates of the population based on the triple-catch method (Begon 1979) and Jolly's stochastic multiple-recapture method (Poole 1974) were far less than the number of snails seen in the study and were thus discounted.

During the study, the portion of the population judged to be potentially reproductive (i.e., a lip was present on the shell) varied from 24.4 to 48.5 percent (on nine visits when lip data were recorded), with the mean percentage being 37.3 (SD = 8.73). Immature, prereproductive animals thus always formed a majority of the population. Only 26 snails measuring less than 6.50 mm in length and judged to be newborn or less than 1 yr old were seen in the course of the study. The number of snails seen with a shell lip, and thus judged to be sexually mature, was 68.

If our data accurately predict a real relationship between the number of yearling snails and the number of sexually mature animals, then the population exhibited a very low annual fecundity of 26/68, or about 0.4 offspring per adult per year. The fact that only 4 of 26 snails less than 6.50 mm in length were ever seen a second time suggests either a very high mortality in this age group or, possibly, that our search efficiency was low for the smallest snails.

TABLE 4

NUMBER OF *Achatinella mustelina* COLLECTED MONTHLY BY SIZE CLASS

SIZE CLASS (mm)	15 Sep 1974	2 Oct 1974	6 Nov 1974	24 Dec 1974	2 Mar 1975	6 Apr 1975	15 Jun 1975	27 Jul 1975	30 Aug 1975	5 Oct 1975	5 Nov 1975	20 Dec 1975
4.50–5.49	2	1	1	0	0	0	0	1	2	2	2	6
5.50–6.49	1	1	0	2	1	3	0	0	0	0	0	2
6.50–7.49	1	0	2	4	1	0	2	1	2	1	0	3
7.50–8.49	5	3	2	4	3	3	0	3	2	1	1	0
8.50–9.49	0	2	2	3	2	1	2	2	4	4	2	0
9.50–10.49	3	1	4	1	1	0	0	1	2	0	0	0
10.50–11.49	0	0	0	1	1	3	5	4	3	1	0	0
11.50–12.49	0	1	2	2	0	1	2	2	1	4	0	4
12.50–13.49	2	4	5	2	1	0	1	0	0	1	0	0
13.50–14.49	3	5	3	2	4	2	1	0	2	1	1	2
14.50–15.49	3	1	2	1	0	2	3	1	2	1	2	3
15.50–16.49	9	10	4	3	0	2	0	2	2	2	6	3
16.50–17.49	6	10	2	5	5	7	6	4	6	4	3	3
17.50–18.49	8	10	6	8	5	6	6	6	14	15	14	12
18.50–19.49	13	7	5	3	9	8	5	9	10	10	7	9
19.50–20.49	2	2	2	0	0	0	1	1	1	2	1	1
Total	58	58	42	41	33	38	34	37	53	49	42	48
Number recaptured		16	24	25	20	30	28	28	39	41	38	32
Percentage recaptured		27.6	57.1	61.0	60.6	78.9	82.3	75.7	73.6	83.7	90.5	66.7

NOTE: Sampling sessions of 25 January 1975 and 13 May 1975 are not included here, because due to weather conditions, collections were incomplete.

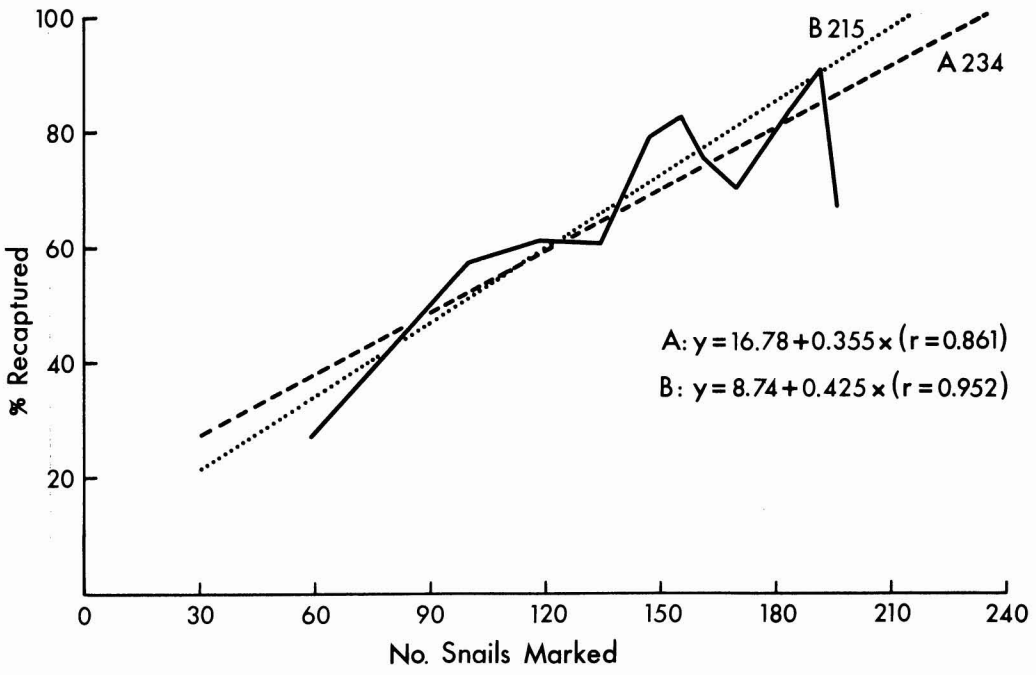

FIGURE 4. Percentage of marked snails recovered versus total number of snails marked (solid line) and regression analyses of the data (broken lines), including (A) and not including (B) the last recapture count. The numbers of snails estimated to be present at 100 percent marking are 234 and 215.

Migration

Twenty snails for which four or more growth intervals were measured were randomly selected for analysis of their migration frequency. In the 100 recaptures of these 20 snails, 51 were in different trees than those in which they had been placed after their prior capture and measurement. When these snails were examined for frequency of tree-to-tree migration as a function of interval duration between recaptures or size of the snail, no correlations were found. Pilsbry and Cooke (1912–1914: xxxv) had suggested that "young shells wandered more widely than the adults." The trees in the study area were close together and the snails could have moved across intermingled branches rather than across the ground.

DISCUSSION

The data presented here strongly support the conclusion that the rate of growth in shell length is constant throughout the growing part of the life-span of an individual of *Achatinella mustelina*. The reasons for this are probably twofold. First, achatinellids are very large at birth, being over 4 mm in length, and their entire life's growth thereafter thus results in less than a fivefold increase in length. A logarithmic phase of growth, characteristic of most very young animals, probably is passed *in utero* in juveniles of *Achatinella mustelina*, if it occurs at all. A second factor contributing to constant rate of length increase up to terminal size is that reproductive maturity occurs after maximum size is achieved. Because there is no major energetic cost due to reproduction until after the shell aperture callus is formed, the end of each snail's growth phase occurs very abruptly, without a lengthy period of asymptotic growth. However, as noted above, the proportions of the shell do change with growth in these snails, and the rate of weight increase may well vary with age, decreasing as animals get older.

The rate of growth observed in *Achatinella mustelina* is very slow as compared with gastropods in general and pulmonates in particular. The giant African snail *Achatina fulica* grows at rates in excess of 24 mm/month during its phase of maximum rate and has an average lifetime growth rate of about 10 mm/month (Kondo 1964). *Cepaea nemoralis* grows considerably more slowly, at perhaps 2 mm/month (Cain and Currey 1967). However, growth is interrupted by aestivation in these snails and the growth is measured in diameter rather than length. Data on age at maturity for two species of *Partula*, land snails from the Society Islands, reared in captivity suggest growth rates of 10–20 mm/yr (Murray and Clarke 1966). Some young, tropical marine gastropods studied by Frank (1969) grew at rates of about 5–10 mm/yr, while others, *Cerithium nodulosum* and *Strombus gigas*, studied by Yamaguchi (1977) and Berg (1976), respectively, grew at rates of 2.7–6.6 and 5–10 cm/yr.

Severns (in press) measured growth in 32 specimens of *Achatinella lila* in captivity for 81 days. Measuring growth along the suture line (i.e., added to the growing shell margin), Severns showed a declining rate of lip growth as shell length increased. Our data on increasing length/width ratios with increased length are in agreement with his data. Severns calculated that animals of 17-mm shell length are 5.27 yr old. This figure is less than our prediction by nearly 2 yr, and may indicate a species difference. However, it does reinforce the fact that achatinellids are slow growing and late maturing.

Reasons for the slow growth rate seen in *Achatinella mustelina* can only be speculative. It may be related either to limited quantities or low nutritional value of the resource on which these snails feed, epiphytic fungi (Pilsbry and Cooke 1912–1914), and to their restricted nocturnal feeding habits. It is possible that calcium for shell growth is only slowly acquired in the snail's diet. It has been suggested (Welch 1938) that feeding may not occur during exceedingly dry periods, and such periods are not infrequent in the Waianae Mountains. However, when we examined our data for evidence of seasonal variation in growth rate, we found none.

The result of a life history pattern such as that seen in *Achatinella mustelina* is well known. Low motility—at least relative to crossing geographical barriers such as valleys and plains—led to great numbers of species arising and the establishment of narrowly localized varieties. More than 200 species were originally described on the basis of relatively consistent morphs. A more realistic count of about 41 species was the result of later revision (Pilsbry and Cooke 1912–1914).

Another result of the life history pattern observed is the vulnerability of populations of achatinellids to predation and habitat destruction. Because of low geographic motility, small isolated populations are readily eliminated. However, a more long-range effect of predation results from the removal of animals during the extended prereproductive phase of their lives. More than 60 percent of the population of *Achatinella mustelina* studied was composed of prereproductive individuals. If predation is random, more than half of the animals removed in a given time period will never have reproduced. Under these conditions, if predation is constant and sufficiently intense, the prey population will eventually die off.

The data presented on the low occurrences of 4.50–6.50-mm juveniles in the study area strongly suggest a low rate of fecundity for the adult individuals of *Achatinella mustelina*—less than one offspring per adult per year. While no observational data are available on the rate of release of offspring by individuals of any species of *Achatinella*, published notes that uteri of adult snails never contain more than two large embryos (Cooke and Kondo 1960, Pilsbry and Cooke 1912–1914, Pilsbry, Cooke, and Neal 1928), and more frequently only one, allow some extrapolation of reproductive rate. If the rate of growth of ova from a fertilized size of 0.75-mm diameter (Solem 1972) to a hatching size of 4.50 mm is similar to that of juvenile snails (about 2 mm/yr), then fecundity would be maximally two offspring per adult per year. Doubling or tripling the growth rate still gives very low fecundity predictions. Presumably, in the native state

the low annual rate of fecundity was offset by a lengthy reproductive life.

Carlquist (1970: 185) notes that "the achatinellas probably had no active predators in prehuman times, although the thrush *Phaeornis* may have eaten a few." The snails were able, apparently, to form dense populations, although it is nearly impossible to arrive at any estimates of density from study of older works based on many thousands of collected specimens. In an undated manuscript, Emerson refers to *Achatinella "duplocincta"* in the "Apex family": "From this one tree about three score of this rare shell were picked." The tree was an ahakea (*Bobea elatior*), a bushy form not exceeding 20 ft in height. By comparison, it seems certain that the population we studied was greatly diminished at the start of our investigation. Consisting of about 220 snails in four trees in a 5 × 5-m quadrat, it was assuredly less dense than those from which dozens of snails were once taken at frequent intervals (Welch 1938).

While our data indicate fairly frequent migration of snails from tree to tree, all published reports on achatinellas suggest that migration occurs too slowly to significantly replenish rapidly depleting populations.

One change that may have occurred between the time of collection of Welch's (1938) specimens and the present was a decline in the mean size of mature snails. Snails from the same ridge system seen by Welch averaged 20 mm or greater in length. The mature snails we saw averaged under 18.5 mm in length. There is no obvious reason for this decline.

The life history pattern of *Achatinella mustelina* can be summarized as that of a species exhibiting slow growth and late maturation, low annual fecundity, large size at birth, and a long reproductive life. Assuming that this pattern evolved in an essentially predator-free situation, the character that appears most obviously as the key to the pattern is the extremely large birth size. At 4.5 mm in length, offspring of *A. mustelina* are nearly one-quarter the size of adults. Such large birth size places severe limits on the size of the maternal organism. Snails reproducing at sizes much less than those seen could only do so by producing smaller offspring.

If growth rate is restricted by nutritional limitations and minimum adult size is limited by juvenile size, then age at maturation must come late. The compensation for low fecundity, itself a consequence of large size of offspring, is an extended reproductive life.

If this interpretation is valid, it becomes of interest to explain the selective advantage of large offspring. A frequently cited factor leading to large birth size is predation focused on small individuals (e.g., Spight 1976). We have no evidence for the existence of an abundance of microcarnivores specializing on snails. A more useful hypothesis favors interspecific competition as a selective force for large birth size in the achatinellas. Literally dozens of species of snails belonging to four families occupy the trees of Hawaii (Zimmerman 1948). Adults of many of these species, in the Tornatellininae for instance (Carlquist 1970), are smaller than the birth size of young of *Achatinella mustelina*. Might not competition with well-developed, small, adult tornatellinins or succineas for resources such as food and space have exerted strong selective pressure against small young in the achatinellas?

The proposition that birth size sets the limit on other life history characters in *Achatinella mustelina* is debatable. We dissected five dried specimens of an unidentifiable species of *Achatinella* and found each to have a single large intrauterine embryo. The largest of these embryos measured 4.35 mm and 4.43 mm in length and were thus in the same size range as young of *A. mustelina* at birth. The snails bearing these embryos had shells 25 and 26 mm in length, contrasting sharply with the mean size of mature *A. mustelina* seen in the present study. Our hypothesis, that extreme selection for large birth size sets a minimum on adult reproductive size, does not explain why snails demonstrably capable of reproducing at 18 mm should grow to 25 mm before reproducing, unless, of course, the large animals belong to a species whose offspring are significantly larger at birth than those of *A. mustelina*.

Perhaps reproductive maturity is age-specific; beyond some minimum size, animals all become reproductively functional at a set age. Size at the onset of reproduction is then a function of growth rate, and that depends on food availability and quality.

A long prereproductive life and low fecundity in species suddenly exposed to massive and diverse predation by a multiplicity of predators (humans, rats, birds, snails) presents a picture of imminent extinction. This is, in fact, the case. When the present investigation was begun in 1974, the study population of *Achatinella mustelina* appeared to be thriving, if not dense. During the course of the study, the population persisted, though numbers may have been declining. One of the native trees in which the snails were found, an *Osmanthus sandwicensis*, died. A few dead snails showing evidence of rat predation were found in the study area at each visit. However, it was the appearance of the introduced predatory snail *Euglandina rosea* that most clearly coincided with the disappearance of all snails from the study site and the ridge above and below it. Specimens of *E. rosea* were first seen on these slopes, below the study area at elevations of about 1000 ft, in December 1974. By 1977 the predatory snails were found near the study site. In August 1979 a reconnaissance of the area showed dead shells of *E. rosea* to be abundant, and living achatinellids, as well as members of all other snail taxa previously seen in the area, were absent. The study area was thoroughly searched for dead shells of *A. mustelina*, and 74 were found, of which only 14 showed breakage similar to that inflicted by rats. It must be concluded that predation by *E. rosea* was the "final" cause of extinction of the population of *A. mustelina* on the Kanehoa trail.

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LITERATURE CITED

BEGON, M. 1979. Investigating animal abundance: Capture–recapture for biologists. University Park Press, Baltimore. 97 pp.

BERG, C. J., JR. 1976. Growth of the queen conch *Strombus gigas*, with a discussion of the practicality of its mariculture. Mar. Biol. 34:191–199.

CAIN, A. J., and J. D. CURREY. 1968. Studies on *Cepaea*. III. Ecogenetics of a population of *Cepaea nemoralis* (L.) subject to strong area effects. Phil. Trans. R. Soc. Lond., B, 253:447–482.

CARLQUIST, S. 1970. Hawaii: A natural history. Natural History Press, Garden City, N.Y. 463 pp.

COOKE, C. M., JR., and Y. KONDO. 1960. Revision of Tornatellinidae and Achatinellidae (Gastropoda, Pulmonata). Bull. B. P. Bishop Mus. 221:1–303.

EMERSON, O. P. Undated. The gay Achatinellidae and their habits. Unpublished manuscript, B. P. Bishop Museum.

FRANK, P. W. 1969. Growth rates and longevity of some gastropod molluscs on the coral reef at Heron Island. Oecologia 2:232–250.

GULICK, J. T. 1905. Evolution, racial and habitudinal. Carnegie Inst. Washington, Publ. 25:i–xii, 1–269.

HART, A. D. 1978. The onslaught against Hawaii's tree snails. Nat. Hist. 87(10): 46–57.

KONDO, Y. 1964. Growth rates in *Achatina fulica* Bowdich. Nautilus 78(1):6–15.

———. 1970. Colloquium on endangered species of Hawaii; extinct land molluscan species. Manuscript. 8 pp.

———. 1980. Endangered land shells, Pacific. Text of a paper delivered to Internat. Union for Conservation of Nature and Natural Resources. 15 pp.

MURRAY, J., and B. CLARKE. 1966. The inheritance of polymorphic shell characters in *Partula* (Gastropoda). Genetics 54: 1261–1277.

PILSBRY, H. A., and C. M. COOKE, JR. 1912–1914. Achatinellidae. Manual of Conchology, Ser. 2,22:i–lviii, 1–399.

PILSBRY, H. A., C. M. COOKE, JR., and M. C. NEAL. 1928. Land snails from Hawaii, Christmas Island and Samoa. Bull. B. P. Bishop Mus. 47:1–49.

POOLE, R. W. 1974. An introduction to quantitative ecology. McGraw-Hill, New York. 532 pp.

SEVERNS, R. M. In press. Growth rate of *Achatinella lila*, a Hawaiian tree snail. Nautilus.

SOLEM, A. 1972. *Tekoulina*, a new viviparous tornatillinid land snail from Rarotonga, Cook Islands. Proc. Malac. Soc. Lond. 40:93–114.

SPIGHT, T. M. 1976. The ecology of hatching size for marine snails. Oecologia 24:283–294.

THWING, E. W. 1907. Reprint of the original descriptions of the genus *Achatinella* with additional notes. B. P. Bishop Mus., Occ. Pap. 3(1):1–196.

VAN DER SCHALIE, H. 1969. Man meddles with nature—Hawaiian style. The Biologist 51(4):136–146.

WELCH, D'A. 1938. Distribution and variation of *Achatinella mustelina* Mighels in the Waianae Mountains, Oahu. Bull. B. P. Bishop Mus. 152:1–164.

———. 1942. Distribution and variation of the Hawaiian tree snail *Achatinella apexfulva* in the Koolau Range, Oahu. Smithsonian Misc. Coll. 103(1):1–230.

WILBUR, K. M., and G. OWEN. 1964. Growth. Pages 211–242 *in* K. M. Wilbur and C. M. Yonge, eds. Physiology of Mollusca. Vol. 1. Academic Press, New York.

YAMAGUCHI, M. 1977. Shell growth and mortality rates in the coral reef gastropod *Cerithium nodulosum* in Pago Bay, Guam, Mariana islands. Mar. Biol. 44:249–263.

ZIMMERMAN, E. C. 1948. Insects of Hawaii. Vol. 1. Introduction. University of Hawaii Press, Honolulu. 206 pp.